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THE GENUS *OREOSTEMMA* (ASTERACEAE: ASTEREAE)

Guy L. Nesom

Department of Botany, University of Texas, Austin, Texas 78713 U.S.A.

ABSTRACT

A group of taxa of western North America that have most recently been treated as a subgenus within *Aster* is here regarded as the separate genus *Oreostemma*: **O. peirsonii** (Sharsmith) Nesom, *comb. nov.*, *O. elatum* (E. Greene) E. Greene, and *O. alpigenum* (Torr. & Gray) E. Greene (the generitype). Three varieties are recognized within *O. alpigenum*: var. *alpigenum*, var. **andersonii** (A. Gray) Nesom, *comb. nov.*, and var. **haydenii** (Porter) Nesom, *comb. nov.* *Oreostemma* is anomalous within *Aster*, but a close morphological similarity, however, is noted between *Oreostemma* and the primarily South American genus *Oritrophium*.

KEY WORDS: *Oreostemma, Aster*, Asteraceae, Astereae

Recent taxonomic overviews of the genus *Aster* L. have recognized a group of three species from the western United States as *Aster* subg. *Oreostemma* (E. Greene) Peck (Jones 1980) or *Aster* "subg. *Oreastrum*" (Semple & Brouillet 1980). In a revisionary treatment of the group, Cronquist (1948) also treated these species within *Aster*, while confirming their status as a natural group. The first described species among them (see citations below), however, was placed in *Haplopappus* DC. (as *H. alpigenus*) by Torrey & Gray, who judged that its closest relatives were among those of *Haplopappus* sect. *Pyrrocoma* (Hook.) H.M. Hall. In the description of the second species (*Erigeron andersonii*), Gray offered the following comment (1865, p. 540): "This is a North American representative of the Andine group of species, sometimes referred to *Aster*, which Schultz has recognized as identical with *Celmisia* [Cass.], and Weddell has referred to *Erigeron* [L.]." These primarily South American species are now identified as the genus *Oritrophium* (Kunth) Cuatr. (Nesom 1992a). Gray soon became dissatisfied with the disparity of this latter species with North American *Erigeron* and transferred it to the highly heterogeneous

Aster sect. *Orthomeris* Torr. & Gray, there placing it closest to species now treated as the genus *Xylorhiza* Nutt. A short time later, with more collections at hand, he also transferred *H. alpigenus* to *Aster*, noting that its rays were violet, not yellow, and offering the following observation (1872, p. 389): "The species is nearly allied to *A. andersonii*, Gray; and with *A. pulchellus* of Eaton (just published in the Botany of King's Exploration), we have now three subscapigerous species of this group." Formal taxonomic recognition of this small group of species was first provided by E.L. Greene (1896, 1900), who treated it at generic rank as *Oreostemma* E. Greene (see nomenclature below).

Greene (1896) noted that the plants of *Oreostemma* are "related to *Aster* somewhat less intimately than are their Atlantic American analogues, the species of *Heleastrum* [DC.]," apparently emphasizing their similar production of long, parallel veined leaves that tend to be basally disposed. Plants of *Heleastrum*, however, are very different from *Oreostemma* in their cormoid rhizomes, leafy stems with densely spaced peduncular bracts subtending the involucres, capitulescences primarily corymboid but sometimes reduced to a spicate arrangement, even more rarely further reduced to a single head, phyllaries with a well defined, basally truncate apical patch, and pappus bristles with dilated apices. It seems improbable that the two taxa are closely related.

Cronquist (1948) stated that the *Oreastrum* group is "clearly related" to *Aster occidentalis* (Nutt.) Torrey but provided no details of justification. The latter species has most recently been hypothesized to be closely related to *A. ascendens* Lindl., *A. chilensis* Nees, and others, treated by Jones (1980) within subg. *Symphyotrichum* (Nees) A.G. Jones. Nor has the *Oreastrum* group been considered in detailed studies of the *A. occidentalis* complex (*e.g.*, Dean & Chambers 1983; Allen 1984). In the phylogenetic analysis of *Aster* sensu lato by Jones & Young (1983), *Aster* subg. *Oreostemma* (as they treated it) was phylogenetically coordinate with their "*Galatella* s.l.;" *Oreostemma* and "*Galatella*" in turn together formed the sister group to the entire remainder of *Aster*. The taxa composing "*Galatella*" sensu Jones & Young are now hypothesized to be more closely related to the goldenaster lineage (the genus *Ionactis*, Nesom & Leary 1992; Nesom 1992b; Nesom 1991b) and the Solidagininae (sensu Nesom 1991b, in press, in prep.). Plants of *Oreostemma* do not produce strongly keeled phyllaries, disc corollas with long, recurved coiling lobes, a double pappus, or *Solidago*-type collecting appendages of the disc style branches, features that would link them to taxa placed in the goldenaster or *Solidago* lineages. After the dispersal of the taxa of "*Galatella* s.l." sensu Jones & Young to genera outside of *Aster* (Nesom in prep.), *Oreostemma* remains one of the disparate, apparently basal elements of the *Aster* alliance, without features that would clearly ally it with other of the Old World or New World groups remaining in *Aster* sensu lato. Jones & Young (1983, p. 78) noted that *Oreostemma* is "The one group emerging on this cladogram [their Fig. 2] as a seemingly well-founded segregate from *Aster* ...;" in their summary diagram

of the phylogeny of *Aster* (their Fig. 5), they placed *Oreostemma* as one of the seven major groups of the genus, each of the latter independently derived from a "hypothetical common ancestor."

Recent consideration of the genus *Oritrophium* (Nesom 1992a) has brought into focus its similarity to *Oreostemma*, substantiating Asa Gray's original observation. Plants of *Oritrophium* are distinctive in their base chromosome number of $x=9$ and their perennial, herbaceous habit, basal rosettes of narrow, primarily 1 or 3 nerved leaves arising from a short, thick rhizome, vestiture of long, thin hairs (Type B trichomes, see below) commonly produced by the lower petioles, monocephalous stems, noncarinate phyllaries without a distinctly developed apical patch, ray flowers with white ligules, disc flowers with linear style branches, achenes somewhat terete and mostly 5 veined, and a pappus of numerous, slender, barbellate bristles but without a differentiated outer series. *Oritrophium* has been considered a subgroup of *Aster*, and if such plants occurred in the United States, they presumably would still be absorbed within *Aster* (sensu lato) as the sister group of *Oreostemma*. Plants of *Oreostemma* do not produce the long, silky trichomes often found in *Oritrophium* but the primary difference between the two taxa is the production of functionally staminate disc flowers in *Oritrophium*, the disc style branches with a corresponding lack of stigmatic lines.

Oreostemma is a well defined, easily recognized, and accepted natural group, but if it remains within *Aster*, its phylogenetic position is highly ambiguous. In contrast, at least a potential, reasonable sister group to *Oreostemma* has been identified in *Oritrophium*. Further, the recognition of *Oreostemma* as a genus separate from *Aster* is a significant step toward allowing the morphological definition of the latter to become more internally consistent. The three species of *Oreostemma* are distinguished by the features in the technical description below, but the identification of the group is much simpler, as there are no other species within North American *Aster* sensu lato that produce erect caudices bearing monocephalous, scapiform stems. Most of the plants of *Oreostemma* are taprooted, but as observed by Cronquist (1948), forms of *A. alpigenus* show transitions from a taprooted habit to a fibrous rooted one. Plants of all taxa of the genus, however, produce the short, erect caudices. Otherwise within *Aster* sensu lato, taproots are found only in *A. tripolium* L., the annual species of subg. *Oxytripolium* (DC.) Torrey & Gray (sensu Sundberg 1986), and the species of *Brachyactis* Ledeb. All of the latter are fundamentally different from *Oreostemma* in a number of ways. Even if *Oreostemma* were considered to have fibrous roots and a multiheaded capitulescence, it would still remain an anomalous element within *Aster*, as none of the categories identified by Jones (1980) or by Semple & Brouillet (1980) could accommodate these three species.

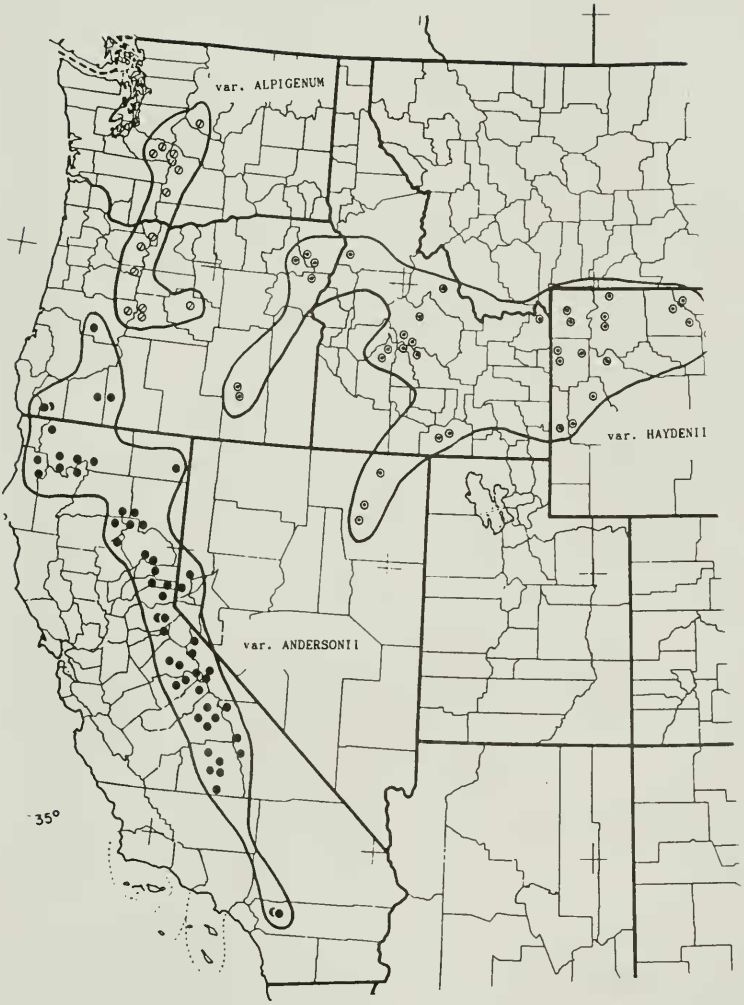
In American *Aster*, outside of the species of *Oreostemma*, monocephalous stems occur only in *A. alpinus* L. var. *vierhapperi* (Onno) Cronq. (subg. *Aster*,

sensu Jones 1980 and Nesom in prep.). In contrast to the superficial habital resemblance, *A. alpinus* differs from *Oreostemma* in the production of relatively slender, fibrous rooted (never taprooted), horizontal rhizomes without a definite caudex, subclasping cauline leaves gradually reduced in size upward, and obovate, strongly flattened, and primarily 2 nerved achenes. *Aster* sensu stricto and *Oreostemma* clearly are not closely related.

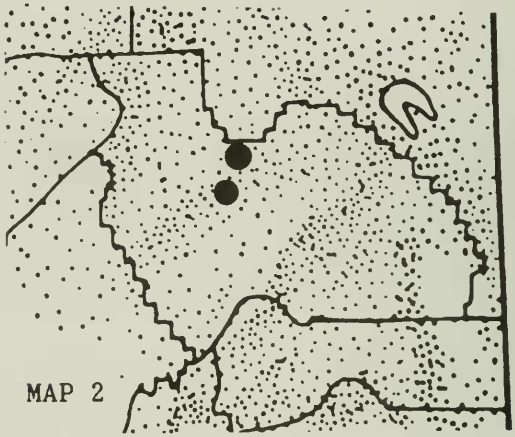
Following Greene's concept, *Aster* subg. *Oreostemma* (the "Oreastrum group") is treated here at the rank of genus. Details of typification are provided in earlier studies (Cronquist 1948; also see Jones & Lowry 1986).

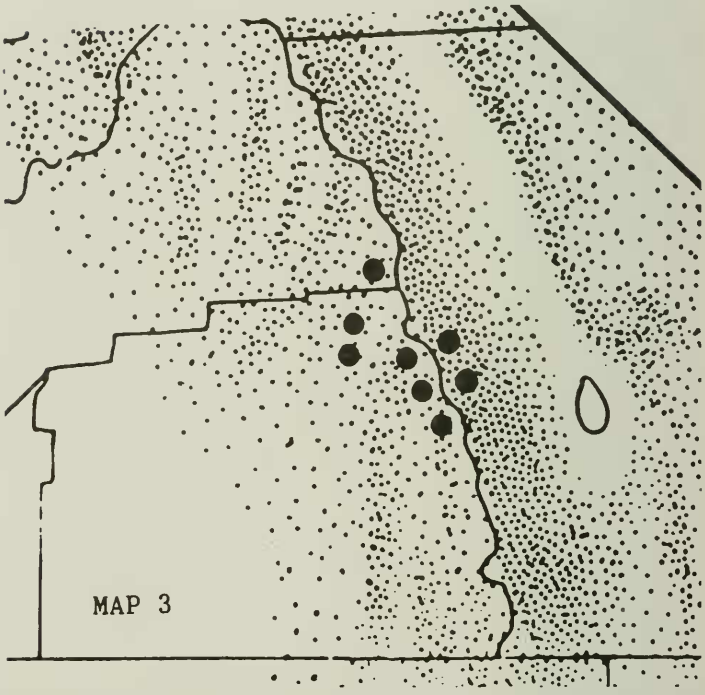
Oreostemma E. Greene [*nom. nov.*], Pittonia 4:224. 1900. Based on *Oreastrum* E. Greene, Pittonia 3:146. 1896. Not *Oriastrum* Poeppig, 1843. *Aster* subg. *Oreostemma* (E. Greene) Peck, *Man. Higher Pl. Oregon* 719. 1941. TYPE: *Oreostemma alpigenum* (Torr. & Gray) E. Greene

Perennials with erect caudices, arising from a stout taproot, often developing erect or ascending caudex branches, less commonly from a short, fibrous rooted rhizome, rarely this developed into a distinctly elongated rhizome. Stems scapiform, monocephalous. Leaves subcoriaceous, entire, the basal in a persistent rosette, narrow, primarily 1 nerved but commonly with a pair of well developed, parallel, secondary nerves, the cauline greatly reduced in size, sessile, slightly subclasping to not at all clasping. Vestiture of stems and leaves (see Nesom 1976): Type B trichomes (uniseriate, thin walled) greatly lengthened, loosely villous, Type A trichomes (uniseriate, thick walled) absent, Type C trichomes (biseriate, usually glandular) abundant in *Oreostemma peirsonii*, absent in the other two species. Phyllaries slightly or not at all keeled, distally herbaceous but sometimes indurated near the base, without a demarcated apical patch, the apices also foliaceous adaxially. Ray corollas white, sometimes purplish, the ligules coiling. Disc corollas with deltate, erect lobes; style branches 2.5-2.8 mm long, the collecting appendages linear narrowly lanceolate, evenly hispid from base to tip, stigmatic lines ca. 1/2-1/5 as long as the appendages (in *O. alpigenum* and *O. elatum*, appendages 2.0-2.2 mm long, stigmatic lines 0.4-0.5 mm long; in *O. peirsonii*, appendages 1.5-1.8 mm long, stigmatic lines 0.7-0.9 mm long). Achenes 4-5 mm long, narrowly oblong, subterete to slightly compressed, with 5-10 thin, superficial nerves; carpopodium mostly symmetric; pappus a single series of ca. 25-40, slender, terete to slightly flattened bristles. The pappus of these taxa was described as double (Jones & Young 1983), but as observed by Cronquist (1948), the upwardly protruding, duplex achenial hairs may give the appearance of an outer series. Chromosome numbers of n=9 and n=18 have been reported for *O. alpigenum* (Huziwara 1958; Raven *et al.* 1960; Semple *et al.* 1983, 1989, 1992), all counts apparently for var. *andersonii*. Karyotype, "primitive type" sensu Semple *et al.* (1983). Maps 1-3.



Map 1. Geographic distribution of the varieties of *Oreostemma alpigenum*.





Map 2. Geographic distribution of *Oreostemma elatum*; all known records from north central Plumas Co., California.

Map 3. Geographic distribution of *Oreostemma peirsonii*; all records from Fresno, Tulare, and Inyo cos., California.

I agree with Cronquist's treatment (1948) of *Oreostemma* (as "the *Oreastrum* group") with respect to the delimitation of the taxa. As treated here, the genus comprises three species, two of them highly restricted in geographic range, the third widespread and variable but divisible into three geographically distinct varieties. As noted by Cronquist (p. 78), "Individual specimens from well within the range of one [variety of *O. alpigenum*] might pass for the other in the absence of geographic data," and populations lying between or at the peripheries of the major portions of the range of each variety also tend to be morphologically intermediate. "In spite of the obvious intergradation, however, a very large proportion of the specimens from the whole range of the [three varieties] can be identified without question from their gross morphology, and the existence of regionally differentiated units can scarcely be denied" (p. 80).

Plants of both var. *alpigenum* and var. *haydenii* are relatively uniform in morphology. Plants intermediate between them in leaf shape occur along the western edge of the range of var. *haydenii* (*e.g.*, the Blue and Wallowa Mountains of Oregon; Cassia and Custer cos. of Idaho). Although some plants in these areas produce distinctly rounded leaf apices similar to var. *alpigenum*, they are mixed with typical var. *haydenii* and have relatively thick leaves more similar to the latter. Similarly, plants from around Breitenbush Lake in Marion Co., Oregon, cited by Cronquist (1948, p. 79) as examples of "true intergradation" between var. *alpigenum* and var. *andersonii*, are variable in achenial vestiture but well within the geographic range of var. *alpigenum* and similar to it in leaf morphology. In turn, small plants of var. *andersonii* might be indistinguishable in leaf morphology from var. *haydenii*. Var. *andersonii*, however, is a great deal more variable in morphology and ecology than either of the other varieties (see key and further comments below). Application of varietal names to plants of *Oreostemma alpigenum* as shown in Map 1 provides the most consistent means of identification.

The following key affirms previous observations regarding distinctions among the taxa of *Oreostemma* and adds some refinement. It is provided here with distribution maps (Maps 1-3) as a companion to the summary and discussion of the taxonomy.

1. Phyllaries, stems, and often the leaves densely invested with short stipitate glands; stems 2-7 cm high. ..... *O. peirsonii*

1. Herbage eglandular, otherwise glabrous or sparsely to moderately villous with thin hairs; stems 4-70 cm high. ..... (2)

   2. Stems, leaves, and phyllaries completely glabrous; phyllaries strongly indurated-stramineous in the basal portion, the outer 1.5-2.0 mm

wide near the base, 3 nerved, the nerves separating the phyllary into 4 longitudinal, indurated bands. ..... *O. elatum*

2. Stems, leaves, and phyllaries densely pubescent to glabrate, but at least some hairs always perceptible on the lower part of the phyllaries and the stem near the head; phyllaries herbaceous from base to tip or slightly tawny indurated in the basal portion, the outer 0.8-1.2 mm wide near the base, 1 nerved. ..... *O. alpigenum* (3)

3. Basal leaves oblanceolate with obtuse to rounded apices, (3-)6-10(-15) cm long, 6-12 mm wide; stems 5-18(-30) cm high. ..... *O. alpigenum* var. *alpigenum*

3. Basal leaves linear-oblanceolate to narrowly oblanceolate with acute apices, 3-12(-35) cm long, mostly less than 6 mm wide; stems mostly 4-15 or 8-40 cm high. ..... (4)

4. Basal leaves (3-)4-9(-12) cm long, (1-)2-4(-6) mm wide; stems mostly 4-15 cm high; achenes mostly hairy only at the apex. ..... *O. alpigenum* var. *haydenii*

4. Basal leaves (3-)8-12(-35) cm long, (1-)2-6(-9) mm wide; stems (4-)8-40(-70) cm high; achenes mostly hairy from base to apex. ..... *O. alpigenum* var. *andersonii*

1. *Oreostemma alpigenum* (Torr. & Gray) E. Greene, Pittonia 4:224. 1900. BASIONYM: *Haplopappus alpigenus* Torr. & Gray, *Fl. N. Amer.* 2:241. 1842. *Aster alpigenus* (Torr. & Gray) A. Gray, Proc. Amer. Acad. Arts 8:389. 1872. *Oreastrum alpigenum* (Torr. & Gray) E. Greene, Pittonia 3:147. 1896.

a. *Oreostemma alpigenum* (Torr. & Gray) E. Greene var. *alpigenum*

Map 1; alpine meadows, commonly in markedly wet or moist areas, lake edges, clearings in subalpine pine-fir woods, less commonly along ridges; 5000-7000(-7500) ft; July-September.

b. **Oreostemma alpigenum** (Torr. & Gray) E. Greene var. **andersonii** (A. Gray) Nesom, *comb. nov.* BASIONYM: *Erigeron andersonii* A. Gray, Proc. Amer. Acad. Arts 6:540. 1865. *Aster andersonii* (A. Gray) A. Gray, Proc. Amer. Acad. Arts 7:352. 1868. *Oreastrum andersonii* (A. Gray) E. Greene, Pittonia 3:147. 1896. *Oreostemma andersonii* (A. Gray) E. Greene, Pittonia 4:147. 1900.

Aster alpigenus (Torr. & Gray) A. Gray subsp. *andersonii* (A. Gray) Onno, Bibl. Bot. 26 (Heft 106):15. 1932. *Aster alpigenus* (Torr. & Gray) A. Gray var. *andersonii* (A. Gray) Peck, *Man. Higher Pl. Oregon* 721. 1941.

Map 1; bogs (sometimes with *Darlingtonia*), marshes, moist to wet meadows, lake edges, pine woods to alpine tundra; (4000-)5000-11,000(-11,500) ft; June-September.

Particularly large plants of var. *andersonii* occur in southwestern Oregon, Nevada, and adjacent California (Sierra and Nevada cos.), where the stems may be up to 65-70 cm tall and the basal leaves up to 35 cm long. Tetraploids have been reported from var. *andersonii* (see above), and it is possible that the conspicuous size increase may be correlated with an increase in ploidy level. Achenes are usually hairy from base to apex, but variants occur throughout the range of the variety, and one collector reported that within a single population, achenes were hairy "throughout to only above" (California, Fresno Co., *Sharsmith 3174*-NY). Cronquist (1948) noted analogous examples of variation within populations of var. *alpigenum*. Plants with filiform leaves are particularly common from Mono Co. south to Tulare Co.; forms with much broader leaves, however, as well as a complete range of intermediates, occur throughout the same area. The variation appears to be between populations rather than within them, but there is no discernible geographic pattern to the variation in leaf morphology, and it seems clear that only a single evolutionary entity is represented.

c. **Oreostemma alpigenum** (Torr. & Gray) E. Greene var. **haydenii** (T.C. Porter) Nesom, *comb. nov.* BASIONYM: *Aster haydenii* T.C. Porter, *Cat. Pl.* 485 *in* Hayden, *Prel. Rep. U.S. Geol. Surv. Montana.* 1872. *Oreastrum haydenii* (T.C. Porter) Rydb., Mem. New York Bot. Gard. 1:398. 1900. *Oreostemma haydenii* (T.C. Porter) E. Greene, Pittonia 4:224. 1900. *Aster alpigenus* (Torr. & Gray) A. Gray subsp. *haydenii* (T.C. Porter) Cronq., Leafl. West. Bot. 5:77. 1948. *Aster alpigenus* (Torr. & Gray) A. Gray var. *haydenii* (T.C. Porter) Cronq., *Vasc. Pl. Pacific Northw.* 5:76. 1955.

Aster pulchellus D.C. Eat., *Bot. King Exped.* 143. 1871; not *Aster pulchellus* Willd. (1803).

Map 1; rocky slopes, talus, ridges, most commonly in alpine tundra but also occurring lower in clearings in pine-fir or pine-spruce woods, sometimes around lake edges or near snow banks but more commonly in drier sites; 8700-11,000 ft; (June-)July-September.

2. *Oreostemma elatum* (E. Greene) E. Greene, Pittonia 4:224. 1900. BASIONYM: *Oreastrum elatum* E. Greene, Pittonia 3:147. 1896. *Aster elatus* (E. Greene) Cronq., Leafl. West. Bot. 5:80. 1948.

Narrowly endemic to northcentral Plumas Co., California (Butterfly Valley and Mt. Dyer), and perhaps immediately adjacent Lassen Co., Map 2; bogs, marshy areas, wet meadows; ca. 3300-5000 ft; July-August.

Cronquist recognized this taxon as a separate species, albeit hesitantly, but I agree with his observations and confirm its distinction from *Oreostemma alpigenum*. *Oreostemma elatum* is represented by few collections, but they are from several localities, made over a period of nearly 100 years (the first in 1875), and the morphology of the plants is highly consistent.

3. **Oreostemma peirsonii** (C.W. Sharsmith) Nesom, *comb. nov.* BASIONYM: *Aster peirsonii* C.W. Sharsmith, Leafl. West. Bot. 5:50. 1947.

Narrowly endemic to the high sierra near the junction of Fresno, Tulare, and Inyo cos., Map 3; rocky slopes, ridges, dry meadows; 10,300-12,250 ft; July-September.

Although *Oreostemma peirsonii* is a narrow endemic, it is represented by numerous collections. It is sympatric with *O. alpigenus* var. *andersonii*, and plants of the two taxa sometimes grow in close proximity. Raven collected both at Wright Lakes, 11,200 ft, in Tulare County and noted a marked difference in habitat: *O. peirsonii*, dry sand (*Raven 8360*-CAS), var. *andersonii*, wet meadow (*Raven 8361*-CAS). No hybrids between the two have been reported, and although scattered individuals of var. *andersonii* may produce a few glands on the phyllaries, there is no clear indication that such plants might be of hybrid origin.

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